1342

Reprinted from PSYCHE, Vol. 90, No. 4, 1983

PSYCHE

Vol. 90 1983 No. 4

THE BIOLOGY OF *MYRMOXENUS GORDIAGINI* RUZSKY, A SLAVE-MAKING ANT (HYMENOPTERA, FORMICIDAE)

By

Alfred Buschinger,[1] Ursula Winter,[1] and Walther Faber[2]

Introduction

Myrmoxenus gordiagini was described by Ruzsky (1902) from material which he had collected in the Akmolinsk area in Soviet Russia, near the town of Koktschetaw. The ant was always found living together with a newly described host species, *Leptothorax serviculus* Ruzsky. The colonies inhabited narrow galleries between and underneath small stones in the rocky slopes of a hilly region, with some birch and spruce trees. Finzi (1924) described a subspecies, *Myrmoxenus gordiagini menozzii*, from the Yugoslavian peninsula of Istria. Only one male and one female were found within moss and soil at the foot of an oak tree, together with numerous females and workers of *Leptothorax unifasciatus* (Latreille). Finzi therefore believed that his new subspecies was living with that host species. Finally, in 1925, Soudek established a new genus, *Myrmetaerus*, for a new species, *microcellatus*, that he had collected near Kotor in Dalmatia, Yugoslavia. Although he explicitly discussed the close relationship of *M. microcellatus* with *Myrmoxenus*, he described this ant as representing a new species and genus "as a provisional arrangement" (Soudek, 1925). *M. microcellatus* was found under a stone in a deciduous forest, in a mixed colony with *Lepto-*

[1]Institut für Zoologie der Technischen Hochschule Darmstadt, Schnittspahnstr. 3, D-6100 Darmstadt, FRG.

[2]Dr. Walther Faber, Vienna, died in June, 1979. Among his papers we found a description of the colony foundation behavior of *M. gordiagini*, and also some important information on localities where he had collected this species.

Manuscript received by the editor June 23, 1983.

B

thorax nylanderi (Förster). All our material also was collected in Istria, and in the Dalmatian island Krk[3]. Since the descriptions of all the three forms mentioned above are nearly identical, we assume that *Myrmetaerus microcellatus* and *Myrmoxenus gordiagini menozzii* are junior synonyms of *Myrmoxenus gordiagini*. We have been unable, however, to check the type material.

Nothing has been known of the biology of *Myrmoxenus*/*Myrmetaerus* except the fact that they were always found living together with a host species belonging to the genus *Leptothorax* Mayr, subgenus *Myrafant* Smith (1950), and thus apparently represent socially parasitic ants. W. Faber in 1972 recorded some observations on their colony foundation behavior. Recently we found out that *M. gordiagini* is a slave-making ant. The results of our experiments are presented in the following sections.

Material and Methods

W. Faber collected a total of three *Myrmoxenus* colonies on 25 May 1972, on the slopes of a small valley NW of Baška, Krk. In the very same locality we found nine additional colonies between September 23 and 26, 1981. Another locality, where we gathered two colonies on 4 August 1976, and one colony on 22 September 1981, is near the ruined town Dva grada, a few kilometers east of Rovinj in Istria, and just 35 km south of the type locality of *M. gordiagini menozzii*. Ten of these 15 colonies contained a *Myrmoxenus* queen; presumably the queens of the other five colonies were either lost during collecting or were missing prior to our collecting. *Myrmoxenus* workers were present in varying numbers up to about 40 (exact numbers cannot be given since all colonies were kept alive for several breeding seasons, and thus produced additional workers). Two colonies contained only a queen and no workers; supposedly they were newly founded.

Male and female as well as worker pupae were present in the colonies collected on August 4, 1976, and a few adult sexuals were found in field colonies on September 22 and 23, 1981.

[3]Recently we found an additional population on the island Rab, south of Krk. Four colonies were collected on October 2, 1983, in an oak forest south of Suha Punta. They contained one queen each, and in one colony we found two additional females that were dealate but not inseminated.

The host species in all 15 colonies was *Leptothorax lichtensteini* Bondroit 1918. Up to about 200 host workers were found in the *Myrmoxenus* colonies. Nest sites were underneath small, flat stones in the soil, or in crevices between such stones. A common, and, in our opinion, quite important character of the *Myrmoxenus* habitats is the fact that they all were situated in rather shady places in a deciduous forest or in the underbrush. We cannot reconstruct the exact experimental device by which W. Faber studied the colony founding behavior. From his records we conclude that the colonies, which he had collected in May, produced sexuals until September. On September 9 and 22, 1972, he noted "strong flight activities," and numerous *Myrmoxenus* females were dealate in the nests and arenas. Several times he put five dealate *Myrmoxenus* females together into the feeding arenas of *L. lichtensteini* colonies. Others were placed into formicaries with different *Leptothorax* species.

Our newly collected colonies from 1976 and 1981 were kept in formicaries and under artificial daily and annual temperature cycles as described by Buschinger (1973, 1974, 1982) and Winter (1979a). For initiating slave raids, we used arenas as depicted by Winter (1979a) and Buschinger et al. (1980). During the raids the room temperature was about 27°C. Contrary to our experiences with *Harpagoxenus* or *Epimyrma*, which need bright sunshine or at least blue sky for raiding, the *Myrmoxenus* seem to prefer a clouded sky. Thus, the first raid which we observed in our labroatory took place on a cloudy day; for the second one, on a sunny day, we closed the window shades.

Colony Founding by *Myrmoxenus gordiagini*

As indicated above, we rely on the quite brief notes of W. Faber, who observed colony founding by *M. gordiagini* females in 1972. According to these notes, the young *Myrmoxenus* queen enters a host species colony (*L. lichtensteini*), apparently soon after mating and dealation, in late summer. Most *Myrmoxenus* females were attacked and often killed by workers of the host species. In a few experiments, however, a parasitic queen survived the attacks and at last was accepted by the host species workers. She then assaulted the host species queen in a very characteristic manner (Fig. 1). She grasped the *Leptothorax* queen's "throat" with her mandibles, and

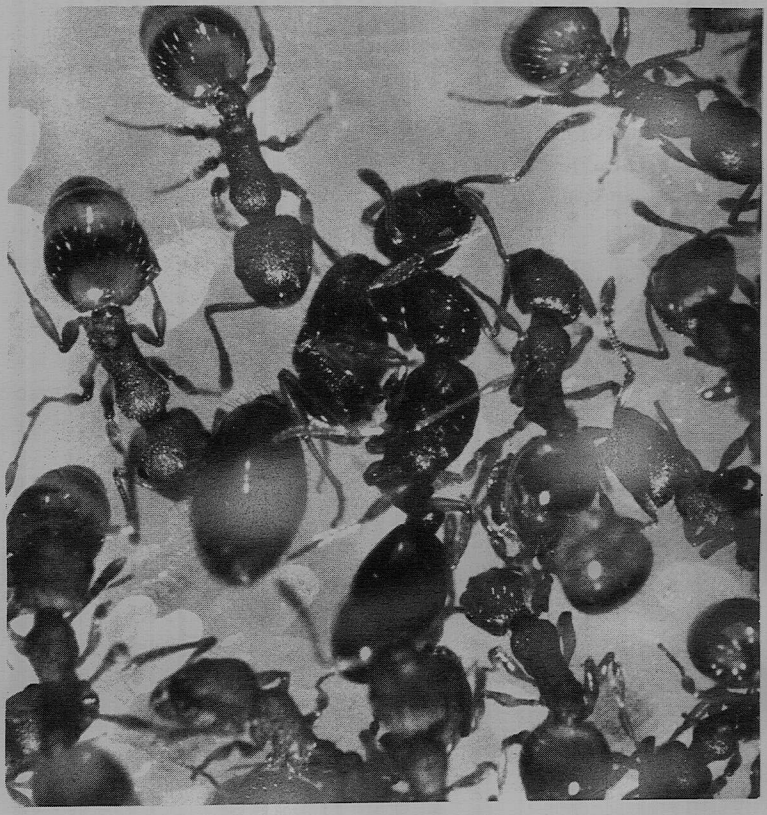

Fig. 1. A queen of *Myrmoxenus gordiagini* (right) is throttling the host species queen during colony foundation (photograph: Faber).

throttled her repeatedly, and often for several hours, as was described for *Epimyrma ravouxi* females (Gösswald 1930). Other *Myrmoxenus* queens were seen to throttle the *Leptothorax* queens by seizing their necks from the back. Like *Epimyrma stumperi* females (Kutter 1951) the *Myrmoxenus* queens also scent themselves by first rubbing their legs over the surface of the victims, and then over their own backs. Sometimes the *Myrmoxenus* queens throttled some host species workers, too, or stung them to death. Furthermore, they attacked the alate *Leptothorax* females which were present in the nests, and killed some of them. In one *L. lichtensteini* colony, where five *Myrmoxenus* females had been put

on September 12, the *lichtensteini* queen was dead on September 17, and one surviving *Myrmoxenus* female was observed to bite the large queen larvae of the host species.

Experiments with *L. parvulus* (Schenck 1852) as host species did not succeed; the *Myrmoxenus* queens were all killed.

Slave Raids of *Myrmoxenus gordiagini*

We observed two slave raids of one *Myrmoxenus* colony, on June 24 and July 7, 1982. The colony was collected in September, 1981. After an artificial hibernation from 12 December 1981, in a constant 6° C until 22 April 1982, the colony began to bring up its larvae. The first prepupae appeared on 4 June, six weeks after the end of hibernation, the first worker and sexual pupae were recorded on 11 June. Sexuals hatched towards mid-July, after the raids, and sexual activity was observed in the beginning of September. A second colony, which was kept under identical conditions, exhibited some scouting activity between June 4 and 25, but did not conduct a raid.

The first colony was put into an arena on 4 June. Simultaneously a colony of the host species, *L. lichtensteini*, was placed into another part of the arena, which was subdivided by a plastic wall.

No *Myrmoxenus* workers were seen outside the nest until 22 June.

On June 23 and 24, between one and three *Myrmoxenus* workers appeared in the arena. Scouting occurred between 1000 and 1500 on June 23. On June 24, a hole in the separating wall of the arena was opened, and a *Myrmoxenus* scout found the way through to the host species territory at 1740. At 1754 this scout ran across the *lichtensteini* nest. It returned to the *Myrmoxenus* nest, entered there at 1804, and suddenly a mass of ants was whirling around inside the nest entrance.

At 1808, a file of about 20 *Myrmoxenus* came out of the nest (Fig. 2) and walked across the arena towards the hole. Sometimes the procession stopped, milling around, apparently until the leading scout had found its way again.

At 1905 the group had reached the entrance of the target nest, and entered it one after the other. Almost no fighting could be observed. After 6 minutes, the *lichtensteini* queen and most of the workers had left their nest, carrying a few small larvae and eggs. Only two *Leptothorax* were stung. Some *Myrmoxenus* workers

Fig. 2. A raiding party of *Myrmoxenus gordiagini* has just arrived at the nest of the host species (photograph: Buschinger).

returned to their own nest, and at 2030 another file of 5 *Myrmoxenus* arrived at the *Leptothorax* nest. By the next morning, the *Myrmoxenus* colony had moved into the former *Leptothorax* nest.

The arena was then subdivided again, and a new *Leptothorax* nest was placed in the position of the former *Myrmoxenus* nest.

The second raid, in the same arena, was observed two weeks later, on 10 July. Scouting began at 0830 and a successful scout returned to the *Myrmoxenus* nest at 0912. However, in this case, a file did not form before 0933. At 1009 a total of 14 *Myrmoxenus* arrived at the target nest, entered it at 1012, and a few minutes later they had overwhelmed the colony and were in possession of its brood. Eight *Leptothorax* were immediately stung to death. Contrary to the first raid, this time the *Myrmoxenus* soon began to carry pupae and large larvae back into their own nest. One returning *Myrmoxenus*, at 1150, led a further file of 15 conspecifics to the raided nest. At 1320 the *Leptothorax* nest was empty except for a few eggs and one *Leptothorax* male. A total of 26 dead *Leptothorax* workers were counted in the arena, indicating that during this raid more fighting had occurred than during the first one.

Discussion

Our results, despite the low number of raids observed, reveal that *Myrmoxenus gordiagini* is a slave-making ant. The organization of

the raids is essentially the same as in *Epimyrma ravouxi* (André) (Winter 1979b, Buschinger et al. 1980), and in the North American *Leptothorax duloticus* (Wesson 1940), with group recruitment and sting fighting.

The colony foundation behavior of *Myrmoxenus* also corresponds to that observed in several species of the genus *Epimyrma* (Kutter 1951, Gösswald, 1930, Buschinger and Winter, in press), where the queens throttle the host species queens.

The only major difference between *Myrmoxenus* and *Epimyrma*, therefore, pertains to antennal segmentation. *Myrmoxenus* females and workers have 12-segmented antennae (males 13), like their host species group, whereas *Epimyrma* has 11-segmented antennae (males 12). We have not yet decided whether this difference can really justify the maintenance of the two genera; however, we are convinced that the very particular raiding and colony foundation behaviors have a monophyletic origin.

We are not entirely certain that *Myrmoxenus gordiagini* is the correct name of our ants. That they are identical with Finzi's *M. g. menozzii* (1924) seems assured, since they were collected in the same area. We are also sure about the identity of this *M. g. menozzii* with Soudek's (1925) *Myrmetaerus microcellatus*. However, if a later revision reveals that *M. gordiagini* Ruzsky and *M. g. menozzii* Finzi were two different species, then our material should be named *M. menozzii*.

The different host species recorded for the three "forms" represent a minor problem. Slave-making ants often have more than one host species. Thus, *Epimyrma ravouxi* (André) enslaves *Leptothorax unifasciatus* (Latr.), *L. nigriceps* Mayr, and *L. affinis* Mayr, sometimes having two slave species together within one colony (Gösswald 1930). It is also quite conceivable that both Finzi and Soudek found their ants, as we did, with *L. lichtensteini* as host species; *L. lichtensteini* has a superficial resemblance to *L. unifasciatus*, and it is quite often confused with *L. nylanderi*.

Summary

Myrmoxenus gordiagini Ruzsky from Dalmatia, Yugoslavia, conducts slave raids with group recruitment and sting fighting.

Young queens enter the host species colonies (*Leptothorax lichtensteini* Bondroit) and kill the *Leptothorax* queens by throttling them. These biological features correspond well with those observed in the genus *Epimyrma*.

Literature Cited

Buschinger, A.

1973. The role of daily temperature rhythms in brood development of ants of the tribe Leptothoracini (Hymenoptera; Formicidae). In: Effects of Temperature on Ectothermic Organisms, ed. W. Wieser, pp. 229–232.

1974. Experimente und Beobachtungen zur Gründung neuer Sozietäten der sklavenhaltenden Ameise *Harpagoxenus sublaevis* (Nyl.). Ins. Soc. **21**: 381–406.

1982. Stock manipulation in leptothoracine ants. Handout prepared for Genetics Workshop (organized by R. H. Crozier), 9th Int. Congr. IUSSI, Boulder, Colorado.

Buschinger, A., Ehrhardt, W., and U. Winter

1980. The organization of slave raids in dulotic ants—a comparative study (Hymenoptera; Formicidae). Z. Tierpsychol. **53**: 245–264.

Buschinger, A., and U. Winter

In press. The reproductive biology of a slavemaker ant, *Epimyrma ravouxi*, and a degenerate slavemaker, *E. kraussei* (Hymenoptera: Formicidae). Entom. Gen. **9**.

Finzi B.

1924. Secondo contributo alla conoscenza della fauna mirmecologica della Venezia Giulia. Boll. Soc. Ent. Ital. **56**: 120–123.

Gösswald, K.

1930. Die Biologie einer neuen Epimyrmaart aus dem mittleren Maingebiet. Z. wiss. Zool. **136**: 464–484.

Kutter, H.

1951. *Epimyrma stumperi* Kutter (Hym. Formicid.), 2. Mitteilung. Bull. Soc. Ent. Suisse **24**: 153–174.

Ruzsky, M.

1902-03. Neue Ameisen aus Russland. Zool. Jb. Syst. **17**: 469–484.

Smith, M. R.

1950. On the status of *Leptothorax* Mayr and some of its subgenera. Psyche **57**: 29–30.

Soudek, S.

1925. Four new European ants. Ent. Rec. **37**: 33–37.

Wesson, L. G., Jr.

1940. Observations on *Leptothorax duloticus*. Bull. Brooklyn Ent. Soc. **35**: 73–83.

Winter, U.

1979a. Untersuchungen zum Raubzugverhalten der dulotischen Ameise *Harpagoxenus sublaevis* (Nyl.). Ins. Soc. **26**: 123–135.

1979b. *Epimyrma goesswaldi* Menozzi, eine sklavenhaltende Ameise. Naturwissenschaften **66**: 581